SOME ASPECTS OF THE ECOLOGY OF MIGRANT SHOREBIRDS. II. AGGRESSION

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THE behavioral patterns of migrant shorebirds differ considerably from those of the same birds on the breeding grounds. The dynamic character of migration and the formation and maintenance of flocks contrasts with the fixed location of the nest site and the lower population densities on the breeding grounds. Population density greatly increases during migration. Species with different breeding ranges or from different habitats join together forming dense multispecific aggregations and frequenting habitats within which all foraging individuals must resort to the same horizontal plane (Recher, 1966).

Aggressive interactions between shorebirds can be observed during both the breeding and the non-breeding seasons, but may occur for very different reasons and have very different effects. During the breeding season aggression is primarily associated with territoriality and courtship. During migration and on the wintering grounds, aggression is primarily associated with interactions between foraging individuals. The density of foraging aggregations and the restriction of individuals to the same horizontal plane creates situations in which some birds may find it difficult to maintain individual distance through avoidance movements and in which the availability of food organisms may be restricted by the presence of competing individuals. Thus it is not surprising that frequent and often prolonged aggressive interactions are a distinctive characteristic of shorebird foraging aggregations during migration.

In this paper we describe the patterns of aggression observed among migrant shorebirds and relate these patterns to prevailing environmental conditions. Some consequences of aggression are also discussed. Descriptions of individual encounters, postures and movements associated with shorebird aggression will be presented elsewhere.

PROCEDURE

The conclusions presented here are based upon observations made between August 1961 and December 1966 along the East, West, and Gulf Coasts of North America. They are primarily concerned with behavior observed in coastal habitats, but probably the conclusions reached are applicable to birds frequenting inland regions.

To provide a quantitative basis for the comparison of aggression under different environmental circumstances, aggressive interactions were scored as to the frequency of occurrence and the intensity of individual events. Intensity is necessarily a subjective evaluation, but to provide a basis for the quantitative comparison of aggressive behavior each display and movement was scored on the basis of time and energy expended and

TABLE 1

INTENSITY VALUES ASSIGNED AGGRESSIVE DISPLAYS AND MOVEMENTS

Intensity Value	Displays and Movements
1.0	Threat display; intention movement; simple supplanting movement (e.g., foraging displacement)
2.0	Displacement movements other than simple supplantations (e.g., defense of individual distance)
3.0	Displacement movements followed by pursuit; displacement movements in which the attacked bird is forced to flight; stand-off displays; pursuit
4.0	fighting

assigned an "intensity value" of from one to four (Table 1). The greater the time and apparent energy expenditure, the higher the assigned value. Because aggressive interactions between individuals might involve any number of separate displays and movements, each interaction was recorded as a series of numbers representing each separate display and movement involved—for example: a threat display followed by a fight and then pursuit would be scored as 1, 4, 3 giving the entire interaction an intensity value of 8. When an interaction involved three or more individuals, the displays and movements of each interacting pair were scored separately—for example: a bird attacked by two others in immediate succession might result in the sequence 1, 3 : 2, 4, 3 giving intensity values of 4 and 9 for each pair's interactions. Translated the 1, 3 might indicate a threat display followed by displacement and pursuit, and the 2, 4, 3 might indicate displacement resulting in a fight followed by pursuit. Appropriate notations were used to keep individuals separate if, for example, the attacked individual became the pursuer.

During periods of observation, censuses were made at a maximum of 5 minute intervals. Whenever possible, the area censused was measured and any noticeable patchiness recorded. (We use the words "patchy" and "patchiness" to indicate the distribution of environmental resources (food and space) as discrete packets or patches.) In the habitats studied, patchiness results primarily from the intermixture of different kinds of substrates, from variations in water content or distribution, and from topographical irregularities.

OBSERVATIONS

Differential Species Aggressiveness.—The frequency of aggression observed during migration varies considerably between species. In part, this is a result of the variable abundance of species—one would not expect to frequently observe aggression between individuals of very rare or uncommon species. But it remains true even among species which are abundant during migration and which form dense foraging aggregations that certain of these (i.e., Red-backed Sandpiper (*Calidris alpina*)[1] and dowitcher (*Limnodromus* spp.)

1 In this paper we have chosen to follow the current B.O.U. Check-list in merging the genera *Ereunetes* and *Erolia* with the genus *Calidris* and the genus *Totanus* with the genus *Tringa*. A variety of behavioral and ecological observations leads us to conclude that this is a more realistic classification than that used in the 1957 A.O.U. Check-list.

are only infrequently aggressive whereas with others (i.e., Western Sandpiper (*Calidris mauri*) and Semipalmated Sandpiper (*Calidris pusillus*)) aggressive interactions are common.

As a result of these species differences, the ideas presented here are based primarily upon observations of Western Sandpipers and Sanderlings (*Crocethia alba*) on the West Coast and of Semipalmated Sandpipers, Sanderlings, and Semipalmated Plovers (*Charadrius semipalmatus*) on the East Coast. Instances of aggression observed between individuals of other species (particularly: Marbled Godwit (*Limosa fedoa*), Willet (*Catotrophorus semipalmatus*), Lesser Yellowlegs (*Tringa flavipes*),[1] Greater Yellowlegs (*Tringa melanoleucus*), Least Sandpiper (*Calidris minutilla*), White-rumped Sandpiper (*Calidris fuscicollis*), Ruddy Turnstone (*Arenaria interpres*), Black-bellied Plover (*Squatarola squatarola*), and Avocet (*Recurvirostra americana*)) have helped in understanding the ecology of aggression. Observations on the infrequent occurrence of aggression among such abundant species as Red-backed Sandpiper and Dowitcher were also of considerable value. They provide a background against which the aggressive behavior of other species stands in bold contrast.

Interspecific Aggressive Interactions.—Aggressive interactions between individuals of different species are normally infrequent and of lower average intensity than intraspecific aggressive interactions occurring simultaneously. Of 926 aggressive interactions scored involving Semipalmated Sandpipers in situations where other species were present, only 4.3 per cent were interspecific. The interspecific interactions observed during the course of this study are presented in Table 2. Undoubtedly, others occurred of which we were not aware and not all of the interactions observed between Semipalmated Sandpipers and Least Sandpipers or between Western Sandpipers and Least Sandpipers were recorded, but the small number of interactions observed for other species pairs do serve to show the infrequency with which interspecific aggression occurs. It most often appears that individuals of different species. if not ignorant of, are at least indifferent to each other's presence. Where interspecific aggression does occur it is usually between morphologically similar individuals in situations of intense intraspecific conflict, as for example, occurs in territorial defense. Sixty-five of the 138 interspecific interactions recorded in Table 2 involve one or more territorial individuals and 88 of 138 involved congeneric birds. Of 126 interactions scored for Western Sandpipers defending feeding territories within multispecific aggregations, 26 per cent were interspecific. All involved the morphologically similar Least Sandpiper.

Despite the increased frequency of interspecific aggression observed to occur during instances of territorial behavior, the average intensity of these

Attacking Bird	Attacked Bird	Number Observed Interactions	Average Intensity
Charadrius semipalmatus	*Charadrius vociferous*	1	1.0
Charadrius semipalmatus	*Calidris pusillus*	1	1.0
Catoptrophorus semipalmatus	*Tringa melanoleucus*	1	1.0
Catoptrophorus semipalmatus	*Crocethia alba*	1	1.0
Catoptrophorus semipalmatus	*Limosa fedoa*	8	1.0
Tringa flavipes	*Tringa solitaria*	5	2.0
Calidris melanotos	*Calidris pusillus*	2	1.0
Calidris fuscicollis	*Charadrius semipalmatus*	2	2.0
Calidris fuscicollis	*Calidris pusillus*	24	1.9
Calidris bairdii	*Calidris mauri*	4	1.0
Calidris minutilla	*Calidris pusillus*	2	2.0
Calidris minutilla	*Calidris mauri*	4	2.5
Calidris alpina	*Calidris minutilla*	3	1.0
Calidris alpina	*Calidris pusillus*	3	1.0
Calidris alpina	*Calidris mauri*	1	1.0
Calidris pusillus	*Charadrius semipalmatus*	1	1.0
Calidris pusillus	*Calidris melanotos*	1	1.0
Calidris pusillus	*Calidris fuscicollis*	4	1.0
Calidris pusillus	*Calidris minutilla*	12	1.9
Calidris pusillus	*Calidris alpina*	3	1.0
Calidris pusillus	*Crocethia alba*	2	1.0
Calidris mauri	*Calidris minutilla*	31	1.0
Calidris mauri	*Lobipes lobatus*	2	1.0
Limosa fedoa	*Catoptrophorus semipalmatus*	5	1.0
Crocethia alba	*Calidris minutilla*	4	1.8
Crocethia alba	*Calidris pusillus*	2	1.0
Crocethia alba	*Calidris mauri*	4	2.0
Crocethia alba	*Calidris alpina*	5	1.6

interactions remains less than simultaneously occurring intraspecific territorial interactions. The average intensity of interactions between Least Sandpipers and territorial Western Sandpipers was only slightly greater than 1.0 whereas the average intensity of intraspecific (Western Sandpiper) interactions occurring simultaneously was 2.5. Of the 41 interspecific aggressive interactions scored involving Semipalmated Sandpipers, 31 occurred in situations where Semipalmated Sandpipers were defending territories. The average intensity of these 31 was 2.0; of the remaining 10, only 1.0. Contrast the average intensity of 2.0 for interspecific interactions involving territorial Semipalmated Sandpipers with an average intensity of 3.0 for 106 intraspecific territorial interactions between Semipalmated Sandpipers.
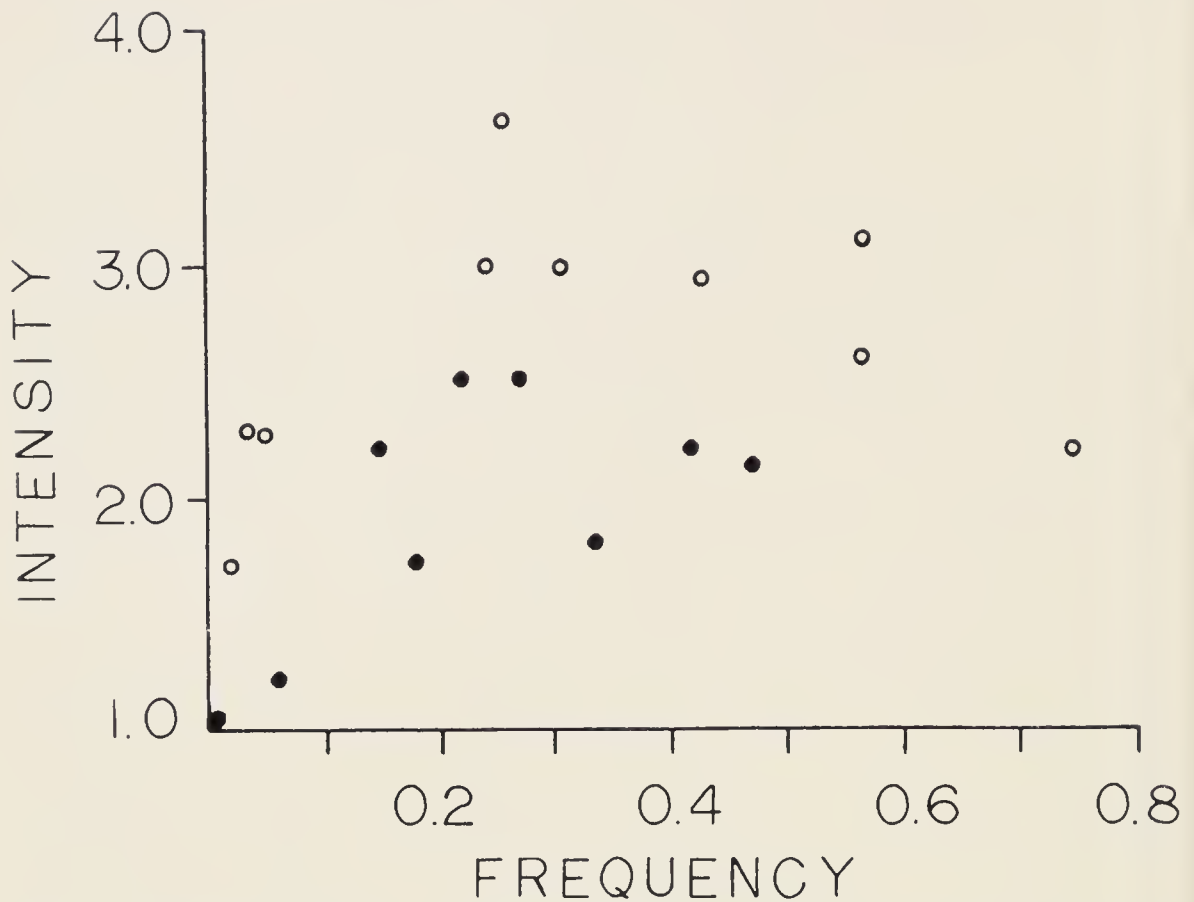
FIG. 1. Relation between frequency and intensity of aggressive interactions. Legend—● Frequency and average intensity of aggressive interactions between non-territorial Semipalmated Sandpipers (*Calidris pusillus*) at Jamaica Bay, New York during August, 1965. Each point represents a minimum of 30 minutes of scored observation. ○ Frequency and average intensity of aggressive interactions between Semipalmated Sandpipers in situations where at least two of the individuals in the observation area were territorial. Each point represents from 5 to 45 minutes of scored observation. Frequency is plotted as the number of interactions observed per minute of observation per individual.

Intraspecific Aggression.—As stated previously, most aggressive interactions occur between conspecific individuals. Species differ in aggressiveness and even between aggregations of species in which aggression is most often observed, the frequency and intensity of aggression varies widely. Within most aggregations of foraging shorebirds, aggressive interactions are limited to low intensity threat displays or supplanting movements, but at any time one may also observe prolonged interactions involving movements and displays assigned high intensity values (e.g., fighting).

In part, the intensity of aggression can be correlated with the frequency of aggressive interactions, while frequency appears to be determined by various environmental conditions.

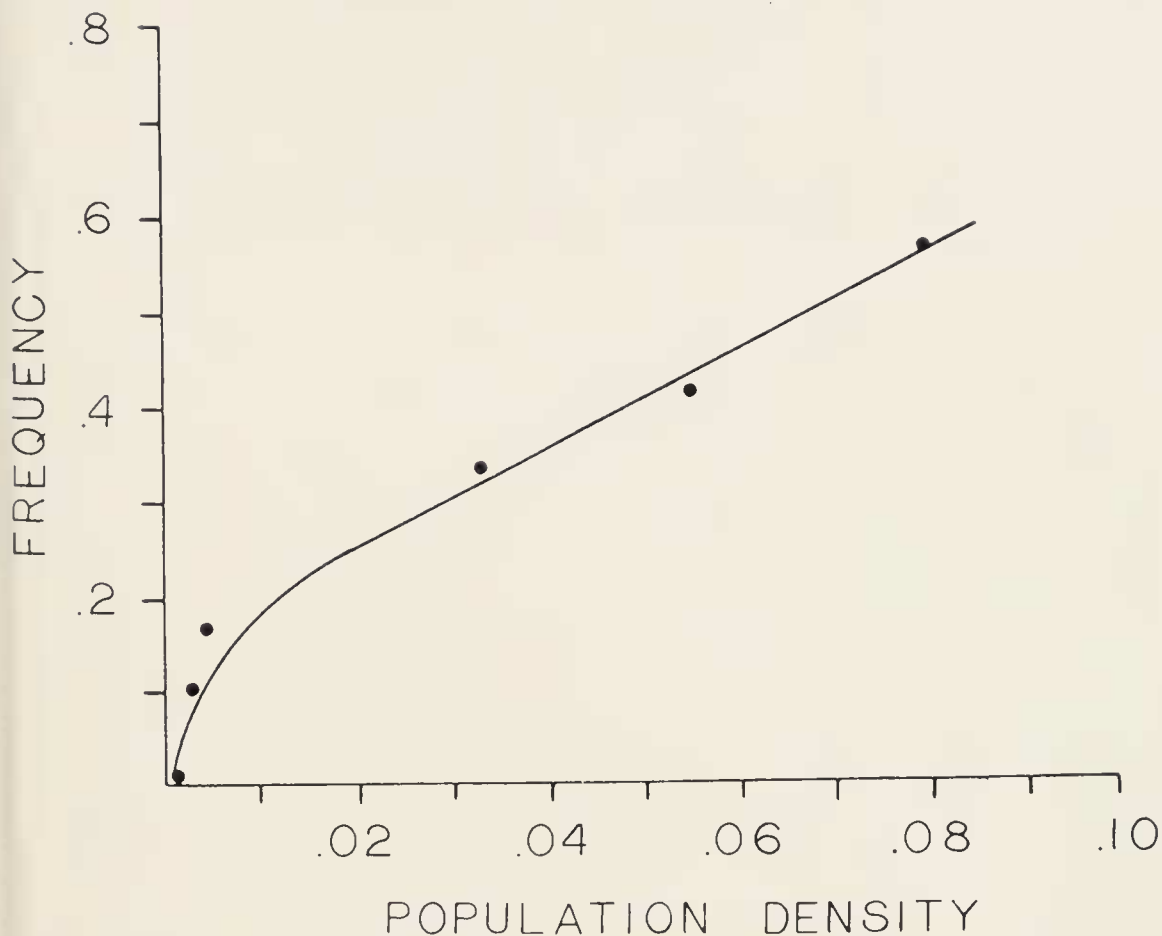*The Relation between Frequency and Intensity of Aggression.*—As the

Fig. 2. Relation between frequency of aggressive interactions and population density. The frequency of aggressive interactions (per individual per minute) between non-territorial Semipalmated Sandpipers (*Calidris pusillus*) at Jamaica Bay, New York has been compared to population density as density increased through migration between 20 and 31 August 1965. The observation site and the area of the observation site remained constant throughout the observation period. Each point represents a minimum of 30 minutes of continuous observation. Population density is represented as individuals per square foot.

frequency of aggression changes or when we compare situations with different interaction frequencies, we find that the average intensity of the interactions observed also changes or differs (Fig. 1). In general, the average intensity of the interactions observed increases as the frequency of aggression increases. However, there is a point beyond which there appears to be a slight but definite decrease in average intensity with a continuing increase in the frequency of interactions. This pattern is also observed in situations where at least some individuals are territorial (Fig. 1).

The observed decrease in average intensity with high frequencies of aggression does not necessarily result from any decrease in interactions assigned high intensity values (for example, fighting or lengthy sequences of displays and movements), but follows from a relative increase in the

number of displays and movements assigned low intensity values (for example, threat displays and supplanting movements). As the frequency of aggression increases a greater number of individuals become involved. Indicative of the greater involvement of individuals is an increase in the number of birds displaying threateningly or bumping and supplanting others within the group. Thus, interactions are more frequent, but of average lower intensities.

Frequency and Population Density.—Normally, the frequency of aggressive interactions is greatest at high population densities and decreases as the population density decreases. In Figure 2, the frequency of aggressive interactions among non-territorial Semipalmated Sandpipers has been compared over a succession of days. The area on which these birds were foraging remained unchanged throughout the period of observation, but the overall population density increased as a result of migration. As may be seen from the figure, the frequency (and consequently the intensity) of aggression increased as the density of the population increased. (The brief span of time covered by these observations makes it unlikely that the observed changes in the frequency of aggression are the result of temporal changes in behavior.) However, there are exceptions to this general rule. Aggression is suppressed at very high population densities and may be reasonably frequent at very low population densities if some of the individuals present are territorial.

Gradual changes in population density such as occurred in the example presented above (Fig. 2) demonstrate quite nicely the overall relation between the frequency of interactions and population density. However, a more frequent situation is the rapid increase in population density following an influx of new individuals or the reduction of the foraging area available on rising tide. In both these instances, the frequency of aggression changes abruptly as the population density rapidly increases as is shown, for example, in Figure 3.

Most often the initial aggressive response to increasing population densities results in the dispersion of individuals, a consequent reduction of population density and a reduction in the frequency of aggression. If population density remains at a higher level than that preceding the influx of new individuals the frequency of aggression may also remain higher, but is invariably lower than that prevailing during the initial aggressive response.

Perhaps the greatest and most consistent concentrations of migrant shorebirds occur along the water's edge on a falling tide. Yet, despite the large numbers of birds aggregated within this relatively narrow zone, aggressive interactions are relatively infrequent. Similarly, large numbers of birds are occasionally seen to aggregate and forage within exceedingly limited areas—presumably they are attracted by an extreme concentration of food
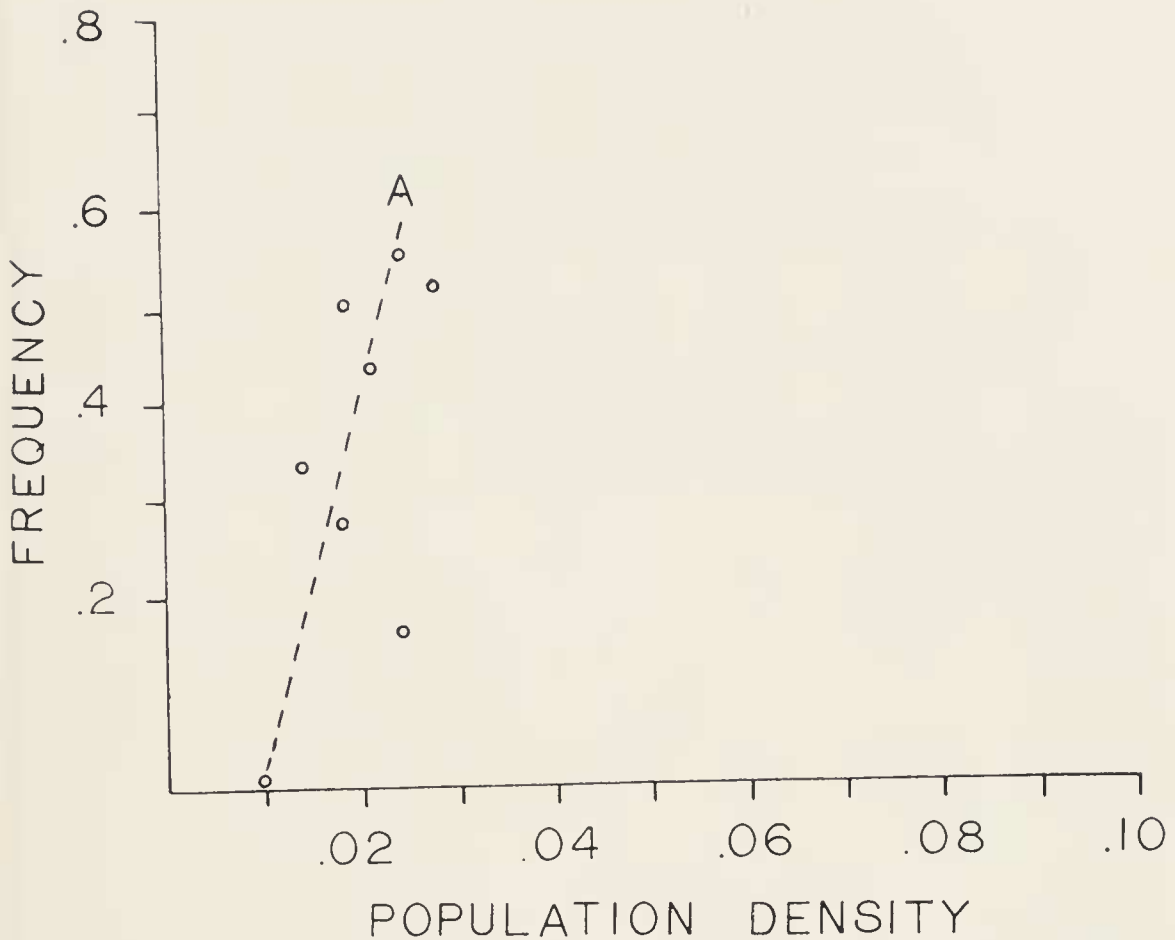
FIG. 3. Relation between frequency of aggressive interactions and population density. Changes in the frequency of aggressive interactions (per individual per minute) between Semipalmated Sandpipers (*Calidris pusillus*) as population density changes abruptly with a decrease in available foraging space on the rising tide at the Brigantine National Wildlife Refuge, New Jersey on 4 August 1964. The points plotted represent consecutive 5 minute scores over a 40 minute period.

organisms—in much the same way as individuals aggregate at a receding water's edge. Here also aggression is suppressed, but may be observed during the initial stages of aggregation and again during dispersal. It is likely that both the extreme population density of these aggregations and the abundance of available food act together to suppress aggression. Brawn (1961) in a study on cod (*Gadus callarias*) observed that the frequency of aggression was depressed while the fish were actually feeding, but shortly after all food was consumed aggression would reappear with "greatly increased vigour."

It is reasonable to presume that once the frequency of aggression exceeds a certain level being aggressive is no longer of benefit to the individual. The individual is therefore confronted with two choices, he may either leave the area or he may cease responding aggressively to the presence of others. If food is particularly abundant (as it is along a tide edge) it is unlikely the

individual will find as good foraging elsewhere and the second choice becomes the better strategy.

Patterns of Intraspecific Aggression.—The local distribution and abundance of migrant shorebirds is, in part, a result of the mutual attraction and repulsion of individuals. Attraction is evident by the failure of individuals to occupy uncrowded or empty areas, preferring instead, to join or remain with others. In contrast, repulsion is represented by the maintenance of individual distance and territoriality. Attraction, like aggression, is most pronounced among conspecific individuals. In multispecific aggregations of foraging shorebirds, individuals tend to associate conspecifically. Single individuals or small groups may temporarily associate with other species, but movements and distribution are normally determined by the physical environment and other conspecific individuals.

Individual Distance.—There is an area around each bird—individual distance—within which other individuals are not tolerated (Conder, 1949). The radius of this area varies, and among migrant shorebirds aggression appears to result when the individual cannot maintain individual distance by avoidance movements and still remain in a suitable feeding area. Aggression is infrequent among shorebirds foraging on very uniform and extensive expanses of tidal mud or sandflat. Where the distribution of suitable foraging area is patchy or restricted as along a water's edge or in a drying marsh, aggressive interactions are more frequent. In the latter situations, individual movements are partially restricted by the patchiness of the habitat and avoidance of other individuals becomes difficult without leaving the foraging area. Patchy environments are also conducive to the establishment of feeding territories.

Avoidance of other individuals becomes increasingly difficult as population density increases. Thus, even when individuals are able to remain in a suitable foraging area, an increase in the level of aggression usually results as population density increases. Population density stabilizes as individuals adjust the extent of individual distance defended with a consequent decrease in the frequency and intensity of aggressive interactions. Because they can adjust the extent of distance defended, individuals are able to forage in areas of higher population densities without being involved in continuous aggression. The ultimate population density which results, depends upon the extent to which individual distance is restricted. It seems likely that the extent of individual distance defended is, in turn, determined by the distribution and abundance of available food organisms. If food is abundant and uniformly distributed, an individual can probably forage efficiently within areas of very high population density. In such circumstances, an individual will restrict the extent of individual distance defended and the frequency of inter-

individual aggressive interactions will be less than in an area where the available food supply is limited or patchily distributed. In the latter situation, individuals will maintain a greater individual distance and may establish feeding territories. Individuals in such are area will respond aggressively to any increase in population density and except when "overwhelmed" by an influx of a large number of new individuals, will maintain population density at a relatively low level.

Territoriality.—During the non-breeding season, individual shorebirds frequently establish and maintain feeding territories. The establishment and defense of these territories follows a pattern similar to that used by many birds in the establishment and defense of breeding territories. The boundaries of feeding territories are well defined and territorial birds "advertise" their territory by a combination of displays and calls. Individuals defending adjacent territories "recognize" their mutual boundaries and each is "dominant" within his own area. How long a territory is maintained depends in part upon where it is established and in part upon the environmental stimulus initiating territorial behavior. It is obvious that territories established below high tide line cannot be maintained beyond the duration of exposure by low tide. Territories established in non-tidal areas may be maintained for long periods of time being re-established from one day to the next. We have recorded instances in which Western Sandpipers and Willets continuously defended territories in excess of five hours and in which a territory was re-established at the same site for at least three days. Unfortunately, we were not able to determine whether with Western Sandpipers the same individuals were involved in re-establishing territories, but are certain that the same Willet returned each succeeding day of observation. Hamilton (1959) in a study of migrant Pectoral Sandpipers (*Calidris melanotus*) found that territorial individuals returned to their territories each day over a number of weeks. He also observed that only a small percentage of the individuals in the area actually established territories and that these were all male birds. Of five territorial Western Sandpipers collected at Palo Alto, California during fall migration of 1963, three were males and two were females. Our observations on Western Sandpipers, Semipalmated Sandpipers, Sanderlings, Willets, and Semipalmated Plovers indicate that the same individual may be territorial or non-territorial and that territoriality depends largely upon environmental conditions. It is not unusual to observe a territorial bird leave his territory, forage elsewhere and then return to re-establish the abandoned territory.

There are two general situations in which we have observed territorial behavior. The first and by far the most common is in patchy environments where either foraging sites are limited or food organisms patchily distributed. Sanderlings, for example, will defend small patches of substrate turned over

by humans digging on tidal flats for worms or clams. On shallow, drying puddles territories established by Western and Semipalmated Sandpipers are invariably located on the downwind shore whenever the breeze has been sufficiently intense to pile up food organisms along the shoreline. Territories are also established along water edges when the zone suitable for foraging is narrow and, in this sense, the available foraging space is restricted. A second situation conducive to territorial behavior has only been observed with Sanderlings though it should apply to other species as well. Sanderlings foraging along open sandy beaches most frequently form foraging flocks which move along the beach as integrated units. If however, food organisms are scarce, Sanderlings disperse and individuals establish territories. It is predictable that a sparse food supply would elicit territorial behavior. The probability of obtaining the occasional food item appearing at the surf edge decreases as the number of Sanderlings foraging at that point increases. The concentration of food in one situation and its scarcity in another are both readily apparent to the human observer and the advantage gained by the territorial bird despite the expenditure of time and energy necessary for territorial defense seems fairly obvious. (Aggressive interactions involved in territorial defense are generally of greater duration and involve a greater number of displays and movements assigned higher intensity values than are associated with non-territorial interactions (Fig. 1).

Though quantitative evidence is difficult to obtain, an indication of the advantage territorial individuals have over non-territorial individuals was secured in a series of observations made on a group of Sanderlings foraging along a water's edge where *Limulus* were spawning. The spawning area had been subdivided into feeding territories with the result that there were a small number of territorial birds within the spawning area and a larger number of non-territorial birds around the periphery making frequent attempts to cross territorial boundaries and forage within the spawning area. Aggressive interactions between territorial and non-territorial birds were frequent and relatively intense (average intensity 2.4). Both groups of birds expended considerable time and energy in aggressive interactions (the two territorial individuals scored spent 32.4 per cent of their time defending their territories and the four non-territorial birds scored spent 38.8 per cent of their time in actual aggressive interactions), with the important difference being that territorial birds were able to forage between aggressions in an area with a very dense concentration of food (*Limulus* eggs literally covered the substrate surface) whereas non-territorial individuals expended *all* the time between aggressions in non-foraging movements about the periphery of the spawning area. Eventually, non-territorial individuals left this area and resorted to less suitable sites (no concentration of *Limulus* spawn).

Tolerance of Neighbors.—There are situations in which shorebirds (especially Semipalmated Sandpipers, Western Sandpipers, and Semipalmated Plovers) may be very tolerant of other individuals (neighbors) foraging in the same area (i.e., individual distance may not be defended), but in which new individuals (strangers) entering the area are attacked and driven off. We have observed this behavior most frequently in small aggregations (less than 15 individuals) foraging in non-tidal situations where suitable foraging areas are small and patchily distributed. *In effect,* the situation is one in which a number of individuals are defending the same territory—tolerant of each other, but intolerant of strangers. However, there is no co-ordinated group action nor is the composition of the group stable so that the area *cannot* be considered a group territory in the sense of Carrick (1959).

Of 104 aggressive interactions scored involving Semipalmated Sandpipers in situations like that described in the preceding paragraph in which the attacked bird was driven from the group area, 70 involved newly arrived birds. Yet, it appears that this is not a case of individuals "recognizing" one another, but of attacking and driving off any conspecific bird landing within the area. Thus, the few non-group birds who happen to walk into the area are generally tolerated and group individuals flying up and relanding within the area are attacked. Each of the 34 interactions scored between group individuals in which the group bird attacked was driven off involved an individual who had flown up and relanded. Group individuals relanding in the area and attacked were frequently able to defend themselves successfully and remain within the area. In only five instances was a non-group individual able to remain within the area after flying in and being attacked. Generally individuals are attacked by one group member after another until driven from the defended area. A result of this response to strangers and the tolerance of neighbors is a remarkably constant population size within the defended area. In a typical series of five-minute censuses for a group of Semipalmated Sandpipers defending a wet area on a drying marsh at Brigantine, New Jersey, the recorded group size was 7, 7, 6, 7, 6, 7.

DISCUSSION

In an ecological sense, aggression among migratory shorebirds is essentially a response dictated by prevailing environmental conditions whether these be population density or the distribution and abundance of food organisms. It is predictable that aggression should occur in those situations in which the individual benefits from being aggressive.

Presumably for individuals of "non-aggressive" species, aggression does not result in any consistent or significant advantage. Species in which aggression is infrequent tend to be birds which forage by probing into the

substrate. They also tend to forage below the water's edge. In contrast, most aggressive species forage above the water's edge and tend to visually locate prey found on the substrate surface. It is possible that probing birds foraging below the water's edge are utilizing a more abundant or more uniformly distributed food supply. Certainly they have access to a wider vertical zonation of prey than do birds restricted to taking prey from the substrate surface. That individuals which locate prey visually may also compete more directly for food organisms seems also likely. Visual predators will almost certainly be alert for prey over a greater area immediate to themselves than will species which locate prey by probing. Because of this, one should expect visual predators to maintain a greater extent of individual distance and to be more aggressive in the maintenance of this distance.

Alternatively, it may be that probing birds must expend proportionally greater amounts of time and energy in the location of prey than do visual birds. If this is true, then the difficulties associated with relocating a patch of prey and in determining the boundaries of this patch so that it might be effectively defended may so reduce the chance of any possible benefit from aggression as to result in its essentially complete suppression among probing species.

The diversity of the habitats frequented by shorebirds appears inadequate to permit the ecological segregation of morphologically similar species (Recher, 1966). The general lack of interspecific conflict among morphologically dissimilar species, but its relatively high incidence among the morphologically similar Least and Western Sandpipers on the West Coast and Least and Semipalmated Sandpipers on the East Coast bears this point out. Grant (1966) in an experimental study of three morphologically similar sparrows, *Zonotrichia spp.*, found interspecific aggression to be most pronounced between the two most morphologically similar species even though the two species normally frequented different habitats. Such interspecific behavioral interactions may be important in the ecological segregation of species. Of the three sandpipers mentioned above, the Least and Semipalmated and the Semipalmated and Western have broadly overlapping bill measurements, but the Least and Western do not. The Semipalmated and Western Sandpipers occur together in only a small portion of their respective migratory ranges. Unfortunately, where they do cohabit we have no information as to how they interact behaviorally. The relationship of the Least Sandpiper to each the Semipalmated and Western Sandpipers is, however, of considerable interest and one reasonably well worked out. The ecology and behavior of these two species pairs illustrate some of the ways in which interactive behavior may determine species relationships.

On the West Coast, the intrahabitat distributions of Least and Western

Sandpipers broadly overlap whereas on the East Coast Least and Semi-
palmated Sandpipers tend to occupy different habitats and occur together
relatively infrequently (Recher 1966). When they are found together aggres-
sive interactions between Least and Semipalmated Sandpipers tend to be
more intense (though probably no more frequent) than aggressive inter-
actions between Least and Western Sandpipers in similar habitats on the
West Coast (Table 2). It is well known among amateur ornithologists that
along the East Coast the Least Sandpiper is a bird of the marshes while the
Semipalmated Sandpiper "prefers" the more open tidal flats. Similarly,
on the West Coast Least Sandpipers are more often encountered in marshy
situations than are Western Sandpipers, but available marshland is con-
siderably more limited along the West Coast than it is in the east. Therefore,
we suggest that on the West Coast Least Sandpipers are "forced" to utilize
tidal flats more frequently than conspecific birds migrating along the East
Coast. Consequently, contact an interaction between Least and Western
Sandpipers cannot be so easily avoided by habitat segregation as it can be
between Least and Semipalmated Sandpipers. The greater morphological
differences and the lesser intensity of interindividual aggression between
Least and Western Sandpipers may be tangible measures of the degree to
which these two species have interacted in the past. The greater intensity
of aggressive interactions between Least and Semipalmated Sandpipers
demonstrates the intensity of the interaction between morphologically similar
species and may be a prime mechanism in causing habitat segregation. Since
they may segregate ecologically by habitat, Least and Semipalmated Sand-
pipers remain morphologically similar. Undoubtedly, interindividual aggres-
sive interactions have not been the exclusive mechanism in bringing about
or maintaining habitat or morphological differences between shorebird
species, but as Grant (1966) also suggests, they may be important in initiat-
ing and maintaining species differences.

SUMMARY

Frequent and often prolonged aggressive interactions between conspecific individuals
are characteristic of shorebird foraging aggregations during migration and on the
wintering grounds. Aggression does occur between individuals of different species, but
is normally infrequent and of lower average intensity than simultaneously occurring
interspecific interactions. Population density and the patchiness of available food and
foraging space appear to be the main features of the environment determining the
frequency of aggressive interactions. The average intensity of aggressive interactions
appears in turn to be determined by the frequency with which individuals interact.
Aggression does act as a population spacing mechanism, but individuals are aggressive
only because it is a means by which they may appropriate for their own use a portion
of the environment (food or foraging space) which would otherwise be unavailable
to them.

LITERATURE CITED

BRAWN, V. M. 1961. Aggressive behaviour in the cod (*Gadus callarias* L.) Behaviour, 18:107–147.

CARRICK, R. 1959. The contribution of banding to Australian bird ecology, Monograph. Biologicae, 8:369–81.

CONDER, P. J. 1949. Individual distance. Ibis, 91:649–655.

GRANT, P. R. 1966. Preliminary experiments on the foraging of closely related species of birds. Ecology, 47:148–151.

HAMILTON, W. J. 1959. Aggressive behavior in migrant Pectoral Sandpipers. Condor, 61:161–179.

RECHER, H. F. 1966. Some aspects of the ecology of migrant shorebirds. Ecology, 47:393–407.

DEPARTMENT OF ZOOLOGY, UNIVERSITY OF SYDNEY, SYDNEY, N.S.W., AUSTRALIA (PRESENT ADDRESS: DEPARTMENT OF ENVIRONMENTAL STUDIES, THE AUSTRALIAN MUSEUM, SYDNEY, N.S.W., AUSTRALIA, 22 MAY 1967.